"An Experimental Investigation of the Nerve Roots which enter into the formation of the Lumbo-sacral Plexus of *Macacus rhesus*."

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Introduction.

The first part of my task is to express my great indebtedness to Professor Victor Horsley for enabling me to carry out this investigation under favourable circumstances at the Pathological Laboratory of University College, and for his great willingness at all times to criticise the results which I obtained.

In a paper on the functions of the nerve roots which enter into the formation of the brachial plexus of the dog,† I gave an account of the views that have been expressed and the work done in connexion with the limb plexuses. The hypotheses as to their significance advanced by Reil,‡ Scarpa,§ A. Monro,|| Sömmering,¶ and others were

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† 'Phil. Trans.,' 1892.

‡ 'De Nervorum Structurâ.'

§ 'De Gangliis et Plexibus.'

|| 'Observations on the Structure and Functions of the Nervous System.'

¶ 'Anatom.,' Pars quinta.

not alluded to, as they were mere conjectures, unsupported by any substantial evidence. The works of Krause, Schwalbe, Herringham, and Paterson were quoted as evidence of how far the problems connected with this subject have been elucidated by anatomical investigation, and the observations of Erb, Knie, and Thorburn alluded to as showing what advance had been made in the subject by the study of diseased processes in man.

Our knowledge of this subject has been greatly increased by numerous experimental researches, the latest of which is that by Sherrington. As his work is of such recent date and contains a historical account of all previous experimental researches that have been carried out in connexion with the lumbo-sacral plexus, it would be superfluous for me to do more than give a list of references to the various communications on the subject, including that of Sherrington, which list will be found at the end of this paper.

Anatomical Introduction.

The Lumbo-sacral Plexus in the Monkey.

Forgue, who does not mention what class of monkey he is dealing with, represents in diagrammatic form the nerves with the roots from which they are derived as follows:—The anterior crural from the 4th, 5th, and 6th lumbar nerve roots; the obturator from the same roots; and the sciatic from the 5th, 6th, and 7th lumbar and the 1st sacral nerve roots. The 2nd sacral root is also figured as sending a branch to the 1st sacral root before the latter enters the sciatic.

Sherrington describes two chief types of plexus in the monkey (*Macacus rhesus*); what he calls a "postfixed" and a "prefixed." The former is figured as having the following arrangement. The external cutaneous takes its origin from the 3rd and 4th lumbar; the 3rd lumbar also sending a branch to the 4th before the latter enters the anterior crural and obturator nerves, which it does in conjugation with the 5th lumbar root, both nerves also obtaining a filament from the 6th lumbar, while the sciatic is represented as springing from the 6th and 7th lumbar and 1st and 2nd sacral roots.

The representation of the "prefixed" plexus shows the origin of the external cutaneous nerve to be the same as in the "postfixed" type, while the branch from the 3rd to the 4th lumbar root is represented as joining the latter after it has given its branch to the external cutaneous nerve. This branch from the 3rd to the 4th lumbar apparently is supposed to send fibres to both the anterior crural and obturator nerves; these nerves also receiving branches from the 4th and 5th lumbar roots. The sciatic is figured as formed from the 5th, 6th, and 7th lumbar and 1st sacral nerve roots.

That Forgue's representation of the arrangement of the plexus does

not agree wholly with either of the types figured by Sherrington is evident; but further comparison of the descriptions of the two observers is rendered useless by the fact that Forgue omits to mention the class of monkey he made his observations on.

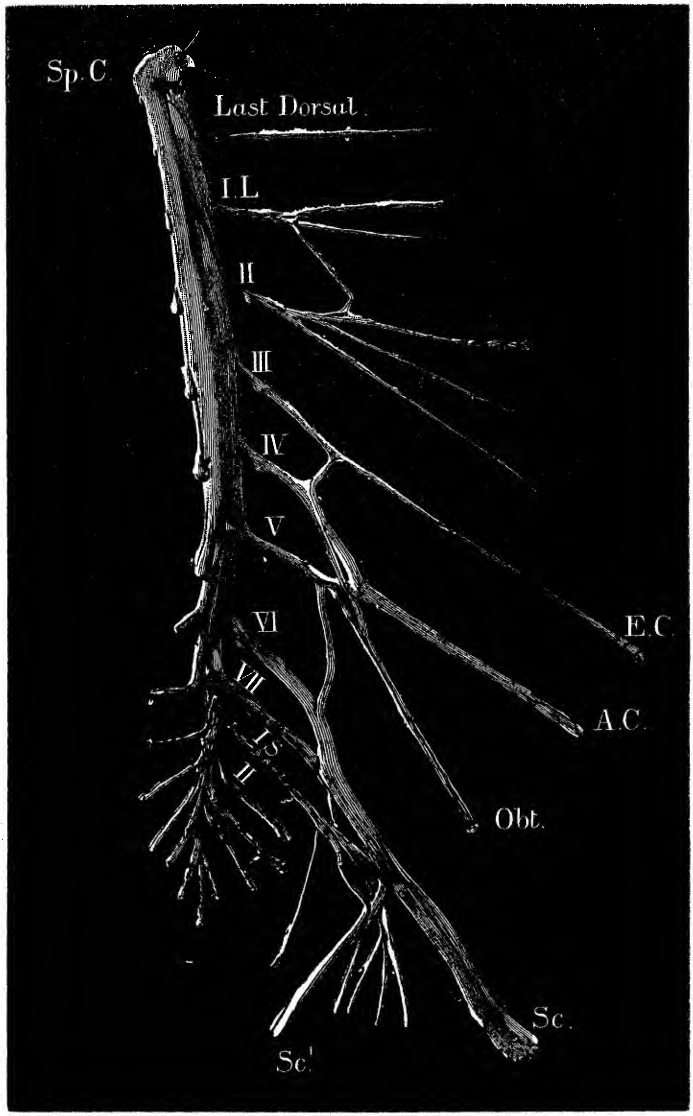
Like Sherrington, I confined myself to *Macacus rhesus* in my experiments on the lumbo-sacral plexus, and from numerous careful dissections, I am compelled to conclude that, at any rate in those animals dissected by me, one type occurred sufficiently frequently to make it necessary to look upon it as the chief one. But at the same time, among the different variations, one was conspicuously more frequent than any of the others, but scarcely sufficiently frequent, I think, to warrant my at present describing two main types, in the way that Sherrington has done.

The arrangement in what has been the most common type in the animals which came under my observation was as follows (see fig. 1) :—The external cutaneous received fibres from the 3rd and 4th lumbar roots; the anterior crural from the 4th and 5th, as did the obturator nerve; and the 6th received a branch from the 5th lumbar root, before its junction with the 7th lumbar root to form the sciatic, which nerve also received a branch from the 1st sacral root. As far as I have seen, the 2nd sacral nerve root never sends a branch to the sciatic, in this type of plexus.

The variation which I have spoken of above as being the most common has the following arrangement (see figs. 2 and 3) :—The external cutaneous is derived from the 3rd and 4th lumbar roots, as in the chief type; but the 3rd lumbar sends a branch to the 4th before the latter gives off its branches to the external cutaneous, the anterior crural, and the obturator nerves. The anterior crural then receives a branch from the 4th and another from the 5th lumbar roots, as in the chief type; but the obturator receives, in addition, a branch from the 6th lumbar root. The sciatic receives no branch from the 5th lumbar root, but only from the 6th and 7th lumbar and 1st sacral roots. I have been unable by the most minute dissections, aided by magnifying lenses, to trace any nerve fibres from the 2nd sacral root to the sciatic trunk. It will be thus seen that the chief points of difference between this and the most common type of plexus consist firstly in the absence of a branch from the 5th to the 6th lumbar root, and therefore to the sciatic; secondly, in the fact that the obturator nerve receives a branch from the 6th lumbar root in addition to those which it receives from the 4th and 5th lumbar; and, thirdly, in that the 3rd lumbar sends a branch to the 4th before the latter gives off any branches to the nerve trunks derived in part from it.

In the plexus of which fig. 2 is an example there can be no doubt that the 2nd sacral nerve root does not send a branch to the sciatic trunk, while that from which fig. 3 is taken shows how in some cases

Fig. 1.



it might easily be erroneously supposed to do so, and how, in such an arrangement, excitation currents might diffuse, with the greatest readiness, from the 2nd to the 1st sacral nerve root, and thus lead to fallacy.

Fig. 2.

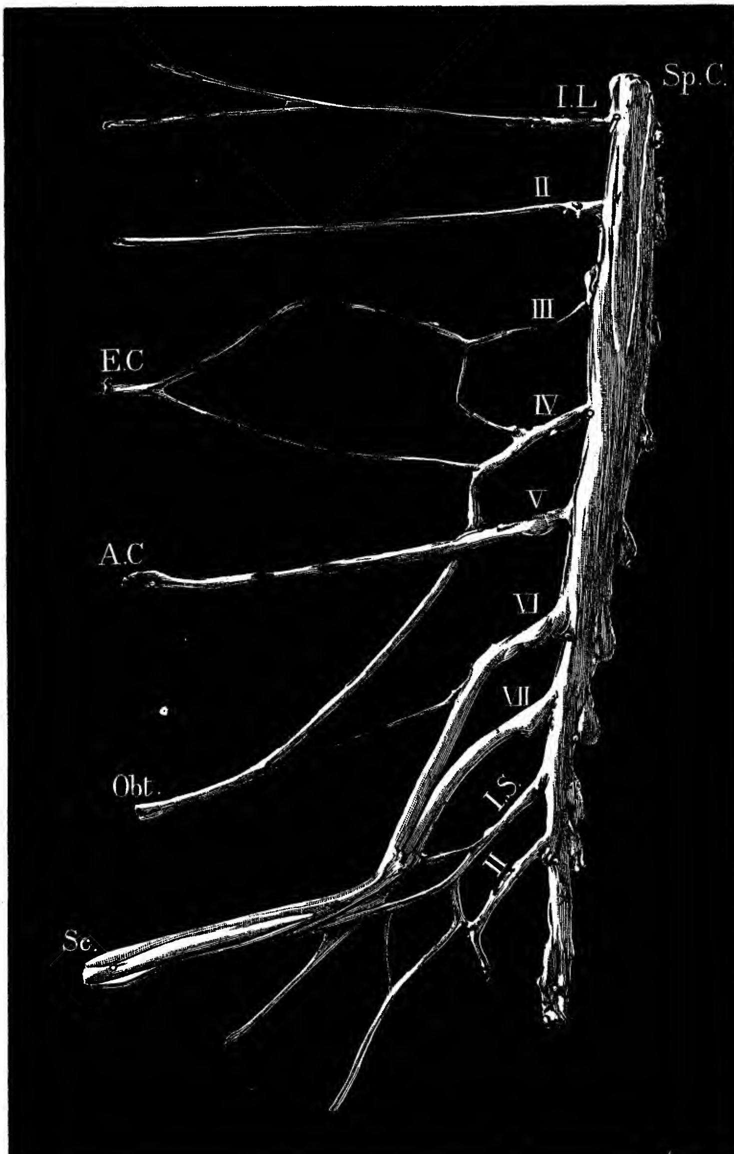
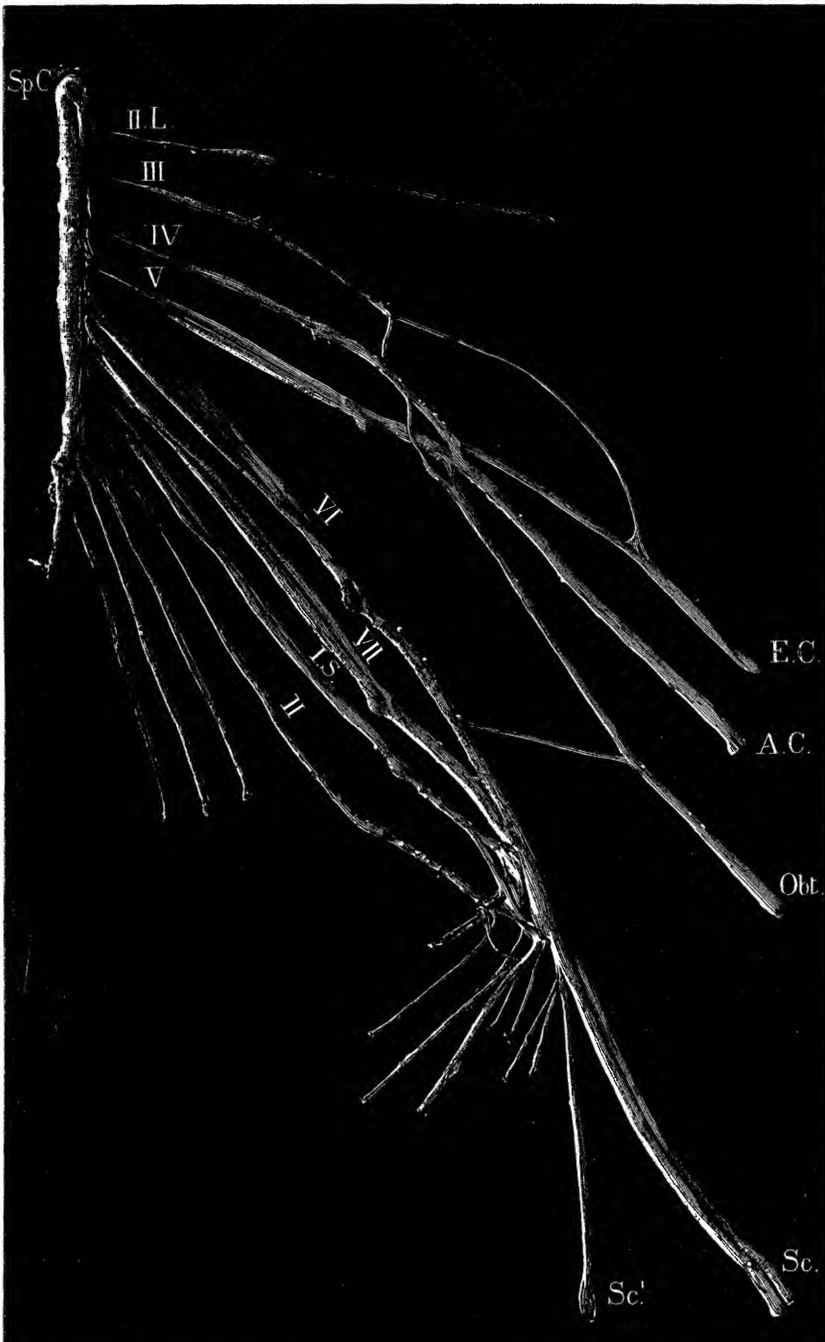


FIG. 3.



The similarity between the plexus which I have found most common and the "prefixed" plexus of Sherrington is obvious; but there is one point of difference. The branch figured by Sherrington as going from the 3rd to the 4th lumbar, and thus taking part in the formation of the anterior crural and obturator nerves, I have not found present. So, too, the variation which I have described as most common agrees with what he calls the "postfixed" type of plexus, with the exception that I have not found a branch from the 6th lumbar to the anterior crural; nor have I found that the 2nd sacral sends a branch to the sciatic. But the number of times I have met with this form of variation have not been sufficiently frequent to justify my denying the existence of such a branch as that from the 2nd sacral root to the sciatic. Indeed, its existence in some cases is rendered very probable by a comparison of this form of plexus with that most commonly met by me in the dog, which resembles it, and in which the 2nd sacral root sends a branch to the sciatic trunk. It is curious that in the species I have examined, the type of plexus most commonly met with in the dog should form the exception in the monkey, while that most commonly met with in the monkey should be the exception in the dog. The fundamental point of difference in the constitution of the two plexuses in the species I have examined has been the presence of a branch from the 5th to the 6th lumbar root in the one form of plexus, and its absence in the other, and it shows that the passage from the one type of plexus to the other is not an abrupt, but a gradual one, for, while in the majority of monkeys examined I found the branch from the 5th to the 6th lumbar root to be large, all graduations were met with down to the most minute filament connecting the two roots (see fig. 4).

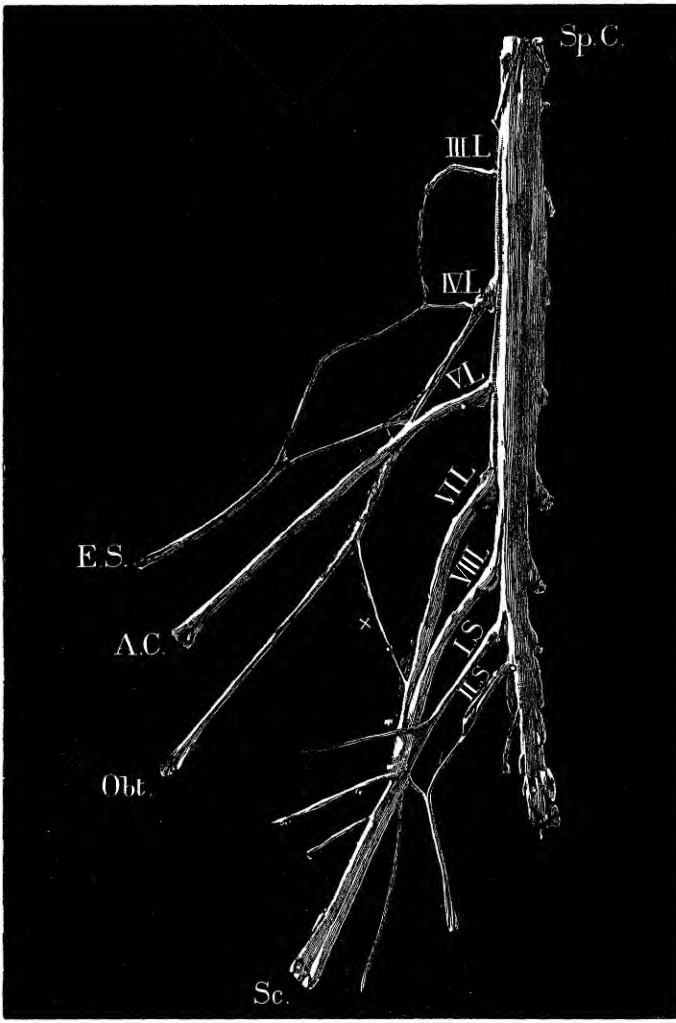
The Muscles of the Posterior Extremity of the Monkey, and their Actions.

In confirmation of Sherrington I find that the muscles of the posterior extremity of the monkey (*Macacus rhesus*) resemble very closely those met with in man; but a few points of difference exist, and must be briefly alluded to.

The gluteus maximus is a very thin flat muscle. There is no evidence of the existence of a peroneus tertius; but peroneo-tibialis muscle is sometimes present. The slip which the abductor hallucis in man occasionally sends to the first phalanx of the second digit is very large and constant, forming a separate muscle in fact.

As was explained in the paper on the brachial plexus of the dog, certain consequences of the action of the muscles deserve careful attention. In studying the mechanism by which the movements are brought about at the various joints, I found that a muscle might bring about a movement at a given joint upon which it has no direct

FIG. 4.



action, and I showed that this is due to the fact that certain muscles pass over more than one joint, and that they are not sufficiently long to allow of full movement taking place at one of those joints without their mechanically and passively pulling on their attachment on the other side of the other joint or joints. In the fore-limb this difficulty was chiefly encountered in connexion with the triceps, as when traction was made on this muscle, in addition to extension at the elbow joint, there resulted extension of all the lower segments of the

limb, owing to the arrangement of the muscles as has been explained above. So troublesome was this action when the movements at the wrist and digital joints were being studied, that an instrument was devised to exclude the action of the triceps under these circumstances. In the posterior extremity, the action of the quadratus femoris tends to produce, besides extension at the knee, extension at the ankle and of the digits. This action of the extensor muscle of the knee, though well marked in the dog, is much less so in the monkey, so that an assistant could fix the limb in such a position as to exclude this action without the aid of an instrument. It is obviously of great importance that this action of a muscle indirectly upon joints on which it has no direct action should be clearly recognised in all investigations of the movements at a given joint when any single nerve root is stimulated. If one muscle can directly or indirectly produce movements at so many joints, it is clear that we must first eliminate indirect effects of the action of this muscle before we can study the movements at these joints, as produced by the muscles which act directly on them, otherwise we should be led into error.

Operative Procedure.

a. Operation.—In every experiment the animal was narcotised by causing it to inhale ether; it was kept deeply under the influence of the anæsthetic during the whole of the experiment, and killed by an overdose of it at the end, except in those experiments in which the animals were allowed to live for some weeks for the study of the effect of section of nerve roots on its mode of progression and standing, and also to allow sufficient time for the degeneration in the peripheral nerves, consequent on such section of a nerve root, to develop. In these instances the operation, which was always a very trivial one, was done under strict antiseptic precautions, and the small wound afterwards dressed antiseptically. The animals were, of course, narcotised in these as in the other class of experiments. The neural canal was first opened, a ligature passed round the motor and sensory portions of a given nerve root together, as close to the spinal cord as possible, after which the two portions of the root were divided between the ligature and the cord. When the separate bundles of nerve fibres of which a nerve root is composed were under investigation, the whole root was dissected out to a varying distance beyond its point of exit from the neural canal, so as to allow of each separate bundle being separated from the others contained in a nerve root, for as long a distance as possible, in order to prevent diffusion of the current from one bundle of nerve fibres to another during the excitation experiments.

In those experiments in which the muscles were exposed by dis-

section, in order to allow of their being directly observed in action when a nerve root was excited, the spinal cord was always first divided transversely in the mid-dorsal region, so as to preclude all possibility of the animal's being conscious of any pain, a possibility most remote, seeing that it was always kept profoundly under the influence of the anæsthetic in this as in all other experiments on the nerve roots.

When intravenous injections of absinthe were given, a jugular or femoral vein was exposed, and a certain quantity of the essential oil injected into the vein selected, by means of a hypodermic syringe.

b. Excitation.—The distal portion of the divided motor root was separated from its sensory fellow, raised in the air by means of a ligature passed round it, and stimulated by means of fine platinum electrodes attached to the secondary coil of a du Bois Reymond's inductorium supplied by a bichromate cell. Exactly the same apparatus was used in excitation of the cortex cerebri (*vide infra*).

Division of Subject and Analysis of Results.

a. Division of the Subject.

As in the previous research, I approached the question by simple excitation of the peripheral end of the cut root, and observation of the compound movement thus produced forms the first part of the investigation. The next step was to carry out, if possible, a more minute analysis of this combined movement, dividing it into its component factors, *e.g.*, by using minimal currents of excitation, applied to the separate bundles of nerve fibres contained in the nerve root. The strength of current necessary to produce the maximum effect without diffusing to other nerve roots was found on the average to be 500 to 600 on Kronecker's inductorium scale. When minimum strengths of current were used for exciting the separate bundles of nerve fibres of which a nerve root is composed, the secondary coil stood at 40 to 50 on Kronecker's inductorium scale, on an average. But both these readings naturally varied considerably, according as the solution in the battery was fresh or old.

The way in which I was led to suppose that each separate natural bundle of nerve fibres of which a nerve root is composed might represent some simple movement, and that it might be possible to evoke such a simple movement by exciting these separate bundles of nerve fibres by minimal strengths of current, has been fully detailed in my former paper. This minute differentiation is not so easily carried out in the lumbo-sacral roots as was found possible in the cervico-dorsal roots of the dog, owing to the fact that the distance between the points of exit of the various nerve roots and those where they

combine to form the plexus is in most instances too small to allow of the minute bundles of nerve fibres being separated from each other for a sufficient length of their course. I was always able to differentiate several of the movements in each root, but was never able to differentiate all in any given root at the same operation. Another factor which contributes to make this process of minute differentiation so difficult is the delicacy of the nerve roots in the monkey as compared with those of the dog, as injury of the nerve fibres is more difficult to prevent in consequence, in the process of their separation from each other. With these difficulties to contend with, the process of differentiation of the various movements was aided by the division of muscles and tendons. That is, after it had been ascertained that a certain movement at a given joint resulted on excitation of a certain bundle of fibres, these muscles or their tendons were divided, and the same bundle of nerve fibres again excited in order to ascertain whether any other movement could be produced at the same joint, *e.g.*, after flexion at a joint had been produced, the flexor muscles acting on that joint were divided, in order to ascertain whether any fibres representing extension existed in the bundle of nerve fibres under investigation.

This minute differentiation forms therefore the second part of the investigation.

Thus far the investigation dealt with movements; it was obviously necessary to pursue the matter further, and to see upon dissection what individual muscles were innervated by the various roots, or their parts when successively excited. This forms the third part of the work. As a corollary to this latter question, I have attempted to determine to what degree any given root supplies a muscle when the latter is innervated from more than one root, and whether any given muscle fibre is possibly supplied from more than one root.

The necessity of instituting new experiments in control of the results obtained by the foregoing methods led to the institution of the following procedures.

Of these, the first, constituting the fourth part of the investigation, consisted in dividing one or more roots, and then observing what effect was produced thereby in the direction of alteration of the natural gait or movement of the limb in progression and climbing.

Another control method, the results of which are embodied in the fifth part, was devised as follows:—A nerve root was divided (in some cases more than one), general epilepsy was then induced by intravenous injection of the essential oil of absinthe, and the resulting deficient participation in the fit of the limb in relation with the divided root or roots carefully observed.

As a corollary to this part of the subject, I tried whether the results obtained by the last method of experimentation are in any way altered when the root or roots are divided some weeks previously, instead of at the time when the epileptic spasms are induced.

*b. Analysis of Results.**

It was found most convenient and instructive to place together the results obtained in Parts I and II of the former investigation, and I see no reason for altering this method of description in detailing the following results.

Part I. Compound movements obtained by excitation of the whole nerve root.

Part. II. Minute differentiation obtained by excitation of the individual natural bundles of the nerve root.

1*st Lumbar Root.*—No intrinsic movement of the limb.

2*nd Lumbar Root.*—No intrinsic movement of the limb.

3*rd Lumbar Root.*—Slight flexion at the hip.

4*th Lumbar Root.*—Part I. Flexion at the hip, with the thigh adducted and the leg extended at the knee.

Part II. (1)†Flexion at the hip.
(2) Adduction of the thigh.
(3) Extension at the knee.

5*th Lumbar Root.*—Part I. Extension of the whole limb with adduction and internal rotation of the thigh and dorsiflexion of the foot.

Part II. (1) Adduction of the limb.
(2) Extension at the knee.
(3) Dorsiflexion of the foot.
(4) Extension of the digits.
(5) Extension of the hallux.

6*th Lumbar Root.*—Part I. The limb extended at the hip, adducted and rotated outwards; flexed at the knee, with the foot at right angles and everted at the ankle, the digits and hallux being flexed at the distal phalangeal joints.

* These results are based on a large number of experiments, and although variations were met with, the results which appeared to be the most constant are those given here.

† The small numbers in brackets denote the bundles from which a different movement was obtained when such bundles were separated in a nerve root. Only those bundles destined for the supply of muscles of the extremity are noted, which accounts in part for so few bundles being mentioned in connexion with some roots; but the variation in the size of the different roots is also responsible for this.

Part II. (1) Extension at the hip.
(2) Flexion at the knee.
(3) Dorsiflexion at the ankle.
(4) Extension at the ankle.
(5) Eversion of the foot.
(6) Extension of the digits.
(7) Flexion of the digits.
(8) Flexion of the hallux.
(9) Extension of the hallux.

7th Lumbar Root.—Part I. The limb extended at the hip, flexed at the knee, extended at the ankle, with the plantar surface of the foot looking inwards, the digits flexed at their metacarpo-phalangeal joints, and the hallux flexed and adducted into the sole of the foot, beneath the flexed digits.

Part II. (1) Extension at the hip.
(2) Flexion at the knee.
(3) Extension at the ankle.
(4) Flexion of the digits at their metacarpo-phalangeal joints.
(5) Flexion of the hallux.
(6) Adduction of the hallux.

1st Sacral Root.—Part I. Interosseal flexion of the digits, with flexion and adduction of the hallux.

Part II. (1) Flexion of the digits.
(2) Adduction of the hallux.
(3) Flexion of the hallux.

2nd Sacral Root.—No movement in the limb.

Part III. Direct Observation (after Dissection) of Muscles thrown into action by Excitation of the separate Nerve Roots.

I next attempted to ascertain as far as possible which muscles are thrown into action by stimulation of the several nerve roots. In exposing the muscles, great care was taken to separate them from each other, so that any communicated movement of one muscle to another should be avoided, as, unless this is done, it is sometimes difficult to be sure whether a particular muscle is contracting, or whether the movement observed in it is only communicated to it by an adjoining muscle which is in action.

Two plans were followed in this connexion. In one, each root was successively selected, and all the muscles in action on excitation of it were noted, while, in the other, a particular muscle, or group of muscles, was kept under observation while all the roots which contributed to the plexus were separately excited. Thus the results

obtained by the one method could be checked by those obtained by the other. In my former experiments I frequently was able to expose the muscles directly after the animal was killed, because the nerve roots, at the end of a prolonged experiment, retained their excitability for a considerable time, half an hour or more. In these experiments this plan has been abandoned, and exposure of the muscles during life alone relied on.

1*st Lumbar Root.*
No muscle related to the limb.

2*nd Lumbar Root.*
Psoas parvus.

3*rd Lumbar Root.*
Psoas parvus.
Psoas magnus.
Sartorius.

4*th Lumbar Root.*
Psoas magnus.
Iliacus.
Sartorius.
Adductor longus.
Quadriceps extensor.
Gracilis.

5*th Lumbar Root.*
Iliacus.
Gluteus minimus.
Adductor longus.
Adductor magnus.
Quadriceps extensor.
Gracilis.
Tibialis anticus.
Tibialis posticus.
Extensor longus digitorum.
Extensor proprius hallucis.
Tensor fasciæ femoris.

6*th Lumbar Root.*
Adductor magnus.
Hamstrings.
Soleus.
Gastrocnemius.
Tibialis anticus.
Tibialis posticus.
Extensor longus digitorum.

Flexor longus digitorum.
Peroneus longus.
Peroneus brevis.
Extensor longus hallucis.
Gluteus maximus.
Gluteus medius.
Gluteus minimus.
Pyriformis.
Obturator internus.
Obturator externus.
Gemellus superior.
Gemellus inferior.
Quadratus femoris
Popliteus.
Plantaris.

7th Lumbar Root.

Hamstrings.
Gastrocnemius.
Soleus.
Flexor longus digitorum.
Peroneus longus.
Peroneus brevis.
Flexor longus hallucis.
Adductor hallucis.
Interossei.
Gluteus maximus.
Gluteus medius.
Pyriformis.
Obturator internus.
Obturator externus.
Gemellus superior.
Gemellus inferior.
Quadratus femoris.
Popliteus.
Plantaris.

1st Sacral Root.

Intrinsic muscles of the foot.

Corollary to Part III.

In my former paper the question as to whether a single bundle of nerve fibres representing a single simple movement ever remains distinct in a nerve root during its course to the muscles it supplies without inosculating with other motor nerve fibres was considered,

and evidence in favour of an affirmative reply brought forward. The results which have been obtained in the present investigation have been in conformity with this view, so that I see no reason to alter the opinion formerly expressed.

A further point that was determined in this connexion was the question whether, when a muscle receives nerve fibres from more than one nerve root, both nerve roots supply nerve fibres to one and the same muscle fibre, and evidence was adduced to negative this possibility. The following evidence also negatives this view:—The peroneus longus muscle is supplied with nerve fibres from the 6th and 7th lumbar nerve roots, and the maximum contraction which can be evoked on excitation of the 6th root alone was greater than that evoked by stimulation of the 7th root alone; but neither effect was as great as when both roots were simultaneously excited. Another muscle chosen in order to test this point was the sartorius, which is supplied by the 3rd and 4th lumbar roots. When the 3rd root is excited with a minimal stimulus, the resulting contraction of the muscle is limited to its upper part, while similar excitation of the 4th root is followed by contraction of its lower part alone.

Part IV (Control). Alteration in the Action of the Posterior Extremity in Progression in Climbing or in Standing evoked by Section of a Nerve Root.

The following experiments were performed in order to observe the effect of division of one or more nerve roots on the movements of the limb during use in ordinary progression, climbing, &c. I observed the effects produced by division of a single nerve root, of two or three consecutive roots, and of two or three alternate roots on the same side. In no instance did I find that the division of a single nerve root was followed by any alteration in the movements of the limb, such as could be detected by running or climbing, twenty-four hours after the operation. A variable amount of paresis or paralysis of certain movements followed section of two or more nerve roots. Section of two consecutive nerve roots produced a greater effect than section of two alternate roots on the same side, an intermediate root being left intact. The effect in both these cases depended on the size of the roots divided, for even if the roots divided were two consecutive ones, and caused great impairment of any given movement, yet the effect noticeable would be much greater if the roots divided were large than if they were small, for the number of other movements weakened would be greater with large than with small roots. I have never found that the monkey's power of grasping the wire of its cage-house in climbing, after section of the 1st and 2nd sacral roots, has been impaired in such a manner as to be

detectable, but here again the experiment has not been repeated sufficiently frequently in the type of monkey in which, according to Sherrington, the 2nd sacral root supplies a branch to the sciatic nerve, which supplies the intrinsic muscles of the foot.

In no case did section of the 1st and 2nd lumbar roots cause any impairment in the movements of the limb, nor did section of the 2nd and 3rd in combination. When the 3rd and 4th lumbar roots were divided on the same side, flexion at the hip was greatly impaired. Movements at the knee appeared most affected when the 4th and 5th, or 6th and 7th, lumbar roots were divided together on the same side, roots which, as we have seen from the stimulation experiments, are concerned with the movements at the knee. The division of the last two roots mentioned also produced most effect on the movements at the ankle. The movements of the digits were most affected when the 7th lumbar and 1st sacral roots were divided together, roots excitation of which produced these movements. Section of the alternate roots, 3rd and 5th, 4th and 6th, 5th and 7th, 6th lumbar and 1st sacral, in combination, produced very little effect. In some cases it was possible to detect slight impairment of movements, but in others it was extremely difficult to be sure that there was any. If, however, three alternate roots, such as the 3rd, 5th, and 7th lumbar, or the 4th and 6th lumbar and 1st sacral, were divided together on the same side, there was no difficulty in detecting the general impairment of the movements of the limb.

In every case there was rapid improvement. In some this was so great that it was difficult to be certain that any impairment of movement remained, notably where alternate roots had been divided. In others, while most of the movements seemed as well performed as on the opposite side, impairment of a particular movement at a given joint remained, this being the case where two or more consecutive roots had been divided.

These results are in keeping with those which were obtained in connexion with the cervico-dorsal nerve roots of the dog. As in those experiments, reunion of the divided ends of the nerve roots was not the cause of the improvement in motor power, as there was not the slightest sign of any such reunion on post-mortem examination, and I have no other explanation to offer for the improvement in motor power which occurs, other than one of the hypotheses formerly advanced in explanation of the phenomenon. One of these suggested the possibility of a reflex inhibitory effect on the cells of the cortex cerebri by the section of a nerve root or roots, producing at first a greater degree of paralysis than would result from exclusion of the nerve root alone. The other supposed it possible that cortical impressions travelling down to the limb and meeting with a block, owing to the division of the fibres along which they formerly passed,

gradually become diverted, it may be through the anterior horn cells of the spinal cord, along other channels.

Part V (Control). Influence of Section of Root or Roots in excluding part of an Epileptic Spasm induced in the Limb by Intravenous Injection of Absinthe.

In this series of experiments an attempt was made to obtain further information as to the functional relations of the nerve roots to the muscles they supply, by the following method of experimentation. A nerve root was first exposed, but not divided; either a jugular or femoral vein was exposed, and 2 minims of the essential oil of absinthe injected into the vein by means of a hypodermic syringe. In order to evoke subsequent epileptic attacks in the same animal, doses of 1 minim of the oil of absinthe were found sufficient. In some cases, after several injections of absinthe, the excitability of the cortex became sufficiently increased to allow of general epilepsy being evoked by means of the induced current applied to the motor area of the cortex cerebri, a method which rarely succeeds in evoking general epilepsy in the monkey under other circumstances.

The first observation that was made in every instance was one to determine the position assumed by the limb during the general convulsions which followed the introduction of absinthe into a vein. In this way it was easy to exclude any error due to injury of any of the roots during the operation necessary to expose them. The position which the limb assumed when all the nerve roots were intact was one of flexion of thigh on the abdomen, with the leg at right angles to the thigh at the knee joint, the foot dorsiflexed at the ankle, and the digits flexed.

When the 3rd lumbar root was excluded, the position assumed by the limb was the same as on the opposite side on which all the roots were intact, with the exception of the flexion of the thigh on the abdomen being less pronounced.

Exclusion of the 3rd and 4th lumbar roots allowed extension at the hip to predominate over flexion, a result in keeping with the fact that excitation of both these roots produced flexion at this joint; while exclusion of the 5th lumbar root as well allowed flexion at the knee to predominate more markedly over extension. After section of the 6th lumbar on the same side, there was only feeble flexion at the knee, with extension instead of dorsiflexion of the root and flexion of the digits. The only intrinsic movement of the limb during general convulsions when the 7th lumbar was also divided was adduction and flexion of the hallux and flexion of the digits, movements which we have seen resulted on excitation of the 1st sacral root; and when

this root was also divided no intrinsic movement of the limb could be observed during the cortical discharge.

On excluding the 1st sacral root alone on one side, no tangible difference in the positions of the limbs on the two sides could be detected during the general convulsions evoked by absinthe.

Exclusion of the 7th lumbar alone caused an increase of flexion at the hip on that side, owing to the extensors being weakened, while there was more extension and less flexion at the knee, because the hamstrings are represented in this root, marked tibial dorsiflexion at the ankle, as the extensors were enfeebled, and flexion of the digits at the phalangeal joints. When the 1st sacral was divided in conjunction with the 7th lumbar root, the limb assumed exactly the same position as in the last experiment, except that the digits were not so powerfully flexed, and the hallux was not adducted, movements which excitation of these roots evoke. The marked feature which was noticeable after division of the 6th lumbar root, in addition to the two last mentioned, was that there was no sign of movement of the digits or hallux during the convulsions, because, of course, all the roots excitation of which produced movements of these parts were divided.

Combined section of the 5th, 6th, and 7th lumbar roots allowed of flexion at the hip, feeble extension at the knee, and flexion at the digits, with adduction at the hallux, during the cortical discharge. The foot remained quite motionless at the ankle joint, as was to be expected, seeing that excitation of no nerve root other than these produced movement at this joint.

Alternate roots were divided in the following combination, and the position of the limb observed during general convulsions. The 4th and 6th lumbar roots divided together caused flexion at the hip to be less marked, as was flexion at the knee, dorsiflexion at the foot, and flexion of the digits. There was thus a weakening of all the movements which predominated when all the roots were intact.

Section of the 5th and 7th lumbar roots, at the same time, was responsible for more marked flexion at the hip and knee and dorsiflexion of the foot. So that, although one of the roots which supplies the quadriceps extensor and one of those which supplies the hamstrings was divided, the section of that to the former group of muscles was attended with the greater result, for it allowed the remaining flexor root to predominate, so to speak, over the remaining extensor root to a greater extent than did the two flexors over the two extensors before any of the roots were divided.

Corollary to Part V.

It seemed desirable to test carefully the question as to whether section of a root or roots some time previous to that at which the

general convulsions were evoked is attended with the same results as when the section is done at the time when the convulsions are induced. I accordingly divided the 4th and 6th lumbar roots on one side, ten days before the day on which I proposed to excite the cortical discharge; and I divided the same roots on the opposite side at the time when the general convulsions were evoked. The result was that the positions of the two limbs were identical during the convulsions. The result of this experiment was confirmed by similar experiments with different combinations of nerve roots.

This method of experimentation was first employed by me in the investigation of the nerve roots which enter into the formation of the brachial plexus of the dog; and, as I have before pointed out, it serves the double purpose of being a means of checking the results of direct stimulation experiments, and of affording us the power of ascertaining whether elimination of a root does or does not result in incoordination of the remaining combination of movements. The results obtained by its use have abundantly confirmed those obtained by stimulating the individual nerve roots; and also prove that the coordination of the movement produced by the remaining roots is not in the slightest degree affected by the elimination of one or more of them. They also make it clear that there cannot be overflow of nerve impulses through the spinal centres, at any rate to any great extent, *i.e.*, impulses which should reach the muscle through the nerve root that has been divided do not under these circumstances reach them by other commissural channels.

Discussion of Results. Conclusions.

Stimulation Experiments.—A comparison of the results obtained by Ferrier and Yeo, those by Sherrington, and my own, shows that there is considerable difference of opinion as to which is the highest nerve root in the lumbar series excitation of which produces movement in the posterior extremity of the monkey. We are all agreed that flexion at the hip is the first movement of the limb evoked as we excite the lumbar roots from above downwards, but Ferrier and Yeo regarded the 4th lumbar as the first in the series from above down excitation of which caused this movement, whilst Sherrington states that in both types of plexus which he has described this movement was produced by excitation of the 2nd lumbar root, though it was feeble in the case of the "postfixed" class of plexus. In no instance have I observed this movement when the 2nd lumbar root was stimulated, the 3rd lumbar being the first root in the series from above down in which I have observed this movement to be represented.

Extension at the hip Ferrier and Yeo found represented in the 5th

lumbar root, while Sherrington and I have found the 6th lumbar root to be the first from above in which the movement is represented.

Extension at the knee Sherrington places as high as the 3rd lumbar root, while my own observations coincide with those of Ferrier and Yeo, who found the 4th lumbar to be the highest root in which this movement is represented.

We are all agreed that flexion of the knee is first represented in the 6th lumbar root from above, though Sherrington has also found it represented as high as the 5th lumbar root; rarely in the "prefixed" class of plexus, which resembles most the type of plexus I have most commonly met with.

Ferrier and Yeo do not mention dorsiflexion at the ankle as produced on excitation of any nerve root, while Sherrington and I are agreed that the 5th lumbar is the highest in the series in which this movement is represented.

We have all found extension at the ankle to be first represented in the 6th lumbar root from above; but, while Ferrier and Yeo and I find flexion of the hallux and digits first represented in the 6th lumbar root, Sherrington states that it is first represented in the 5th.

With regard to the inferior limit of supply to the limb, Ferrier and Yeo found this to correspond to the 1st sacral nerve root, and this has been the lowest root of the series from which I have been able to obtain any response in the limb.

Sherrington found that in the "prefixed" class of plexus which he has described, this is the lowest limit of root supply to the limb; but that in the "postfixed" class this limit extends as low as the 2nd sacral nerve root (9th post-thoracic root).

The number of times I have met with the type of plexus most resembling that described as "postfixed" by Sherrington has not been sufficiently frequent to justify my expressing any decided opinion as to the inferior limit of root supply to the limb in this class of plexus. All I can say is that I have never succeeded in evoking any intrinsic movement in the limb by excitation of the 2nd sacral root with currents of such strength as elicited movement when applied to other nerve roots, or even with currents very much stronger than this. Only by using such powerful currents that there could be no doubt as to the diffusion of the current beyond the root to which it was applied, was I ever able to elicit any intrinsic movement in the limb. Further, I have failed, by most careful minute dissections, aided by powerful lenses, to trace any nerve fibres from the 2nd sacral nerve root to the sciatic nerve. Of course the crucial test of this point would be to divide the 2nd sacral nerve root in this class of plexus, and observe whether degeneration in the sciatic nerve follows. This I have attempted, but unfortunately the animals in

whom I have divided the 2nd sacral nerve roots have, up to the present, had plexuses resembling the "prefixed" class. I have great difficulty in understanding how Sherrington finds any given muscle represented in so many more nerve roots, as a rule, than I do, and, conversely, how he finds so many more muscles, and, in consequence, movements, represented in certain roots. As an instance, the tibialis anticus is stated to be represented in the 5th, 6th, and 7th lumbar nerve roots, while I have only found it represented in the 5th and 6th lumbar roots. Then, again, the 1st sacral nerve root in the "prefixed" class of plexus, which corresponds most closely to the type of plexus I have most commonly met with, is said to produce extension at the hip with slight rotation outward of the thigh, flexion at the knee, extension at the ankle, strong flexion and abduction of the hallux and flexion of the digits in "interosseous" position; whereas, like Ferrier and Yeo, the only movements I have found most constantly represented in this root have been interosseal flexion of the digits, with flexion and adduction of the hallux.

The only way in which I can account for these very great differences in our results is by supposing that while I have only included those roots in which a given muscle is most commonly met with, and those movements, or muscles, most commonly met with in any given root, Sherrington has included every variation; for, as an example, all the movements mentioned by him as represented in the 1st sacral root, I have found represented in that root in rare instances, but never all represented together in any single animal. The movements most commonly met with in any single animal were those already mentioned, and when variation occurred it consisted in one or other of the other movements being added to these.

If I am correct in my interpretation of Sherrington's classification of results, I cannot help feeling that that which I have adopted is more instructive and less likely to lead to confusion.

With regard to the question whether the limb plexuses have an anatomical or physiological significance, I find it difficult to believe that the developmental processes which bring about these arrangements of nerve fibres do so on a purely anatomical basis without regard for physiological combination. Because excitation of a given nerve root with the induced current evokes a movement which may not resemble a natural one is to me no argument against the possibility that in this nerve root nerve fibres destined for the supply of certain groups of muscles are combined in such proportions as they are likely to be required in certain natural movements. The point is one which is exceedingly difficult to test by experiment, and those instituted by Sherrington with a view to solving this problem do not appear to me to be conclusive.

The facts that muscles or groups of muscles are represented in such

different degrees in different nerve roots, and that one group predominates in one root while another predominates in another, lend strong argument to the probability that the arrangement is in great measure a functional one. If the arrangement of nerve fibres in the nerve roots is a purely anatomical one, why should all the fibres destined for the supply of a given muscle not be contained in the same nerve root? What necessity would there be for the division of the fibres so that one set of them should be contained in one root, while another set is contained in another? These points are strongly opposed to the supposition that such an arrangement has been brought about without any regard for physiological action. Then, also, the fact that muscles which are known to act in consort are represented in the same nerve root is one which it is difficult to interpret by mere anatomical arrangement without regard for physiological laws.

Contrary to the observations of Sherrington, I find that the compound effect obtained on electrical excitation of a nerve root may be resolved into its component factors, when it is found that movements diametrically opposed to each other may be represented in the same nerve root, *e.g.*, flexion and extension.

It seems to me that some of Sherrington's own results point in this direction; for although he makes the statement that each small bundle of nerve fibres in a nerve root represents a miniature root, as it were, yet he finds that by using minimal currents differentiation was obtained in so far that one simple movement was elicited before another as the current was gradually increased in strength. The explanation I would offer for the different conclusions come to on this point by this observer and myself is that he excited the nerve fibres on the proximal side of the intervertebral foramina while I excited them on the distal side. The latter procedure makes it possible to separate the different bundles of nerve fibres contained in a nerve root for a greater distance of their course, and thus to avoid more effectually the possibility of diffusion of the current from the bundles of fibres actually excited to those juxtaposed. I am aware, from my own experience, that it is almost impossible to get any differentiations of movements in a nerve root unless the bundles of fibres of which it is composed be first traced well beyond the intervertebral foramen. That this should be the case is only natural, for what is more likely than that the fibres, packed together so closely as are the bundles of a nerve root in their passage through an intervertebral foramen, should make it very easy for the current applied to one set of fibres to diffuse to others in such close contiguity. That separation of one bundle of nerve fibres from another for a sufficient distance in their course is as important a factor in this differentiation of simple movements as is the use of minimum currents for excita-

tion in this connexion, is proved by the difficulties met with in obtaining differentiation in the case of the nerve roots which enter into the formation of the lumbo-sacral plexus, where the distance between the points of exit of the nerve roots from the neural canal and the point where they unite to form the plexus is not so great as in the case of the cervico-dorsal roots and the brachial plexus, and where, consequently, differentiation is not so easy to effect as in the latter case. If further proof were needed in support of the fact, which I have repeatedly convinced myself and others of, viz., that it is possible to separate the fibres concerned with one simple movement in a nerve root from those concerned with another simple movement, nothing could be more convincing than the results which I obtained with regard to the recurrent laryngeal nerve.* In this small nerve I found that it was possible to separate those nerve fibres concerned with abduction from those concerned with adduction of the vocal cords; so that electrical excitation of the one set of fibres evoked the one movement, while excitation of the other set evoked the other movement. If such differentiation be possible in a nerve of such small size, how much the more likely is it that it should be possible in a nerve root of so much greater proportions; unless it is argued that the structural arrangement of nerve fibres in a nerve root differs from that met with in a nerve trunk. My own observations leave no doubt in my mind that the structural arrangement in a nerve root is identical with that met with in a nerve trunk; and there is, besides, abundant proof of this from the observations of others.†

Such single simple movements bear an almost constant relation to the nerve roots, the same movements being, as a rule, found in any given root, and such movements always bear the same relation to the spinal level, *e.g.*, extension and flexion of the knee are represented together in one root, while extension is represented alone in the root immediately above this, and flexion is represented alone in the root immediately below this.

Each bundle of nerve fibres, representing a single simple movement in a nerve root, remains distinct in its course to the muscle or muscles producing such a movement, without inosculating with other motor nerve fibres. Additional evidence in support of this statement is supplied by the results obtained in the case of the recurrent laryngeal nerve, for in this nerve it was found possible to separate accurately the abductor from the adductor fibres, and to trace them by dissection to the abductor or adductor muscles of the larynx. And when one set of nerve fibres was divided while the other was left

* 'Roy. Soc. Proc.,' vol. 51, 1892.

† *Cf.* Herringham, Paterson, &c.

intact, degeneration resulted in the muscles of corresponding function, and in these alone : those of opposite function showing no sign of degeneration.

The group of muscles supplied by any given nerve root occupy both the anterior and posterior surfaces of the limb ;* in other words, muscles whose unimpeded action would produce one movement are represented in the same root as others whose action would produce a movement diametrically opposite, *e.g.*, the flexor and extensor muscles of the ankle are represented in the same nerve root. In such combinations certain muscles are always more extensively represented than others; so that, with a current sufficiently strong to stimulate all the fibres in a nerve root equally, certain muscles predominate in their action over others. The 6th lumbar root contains fibres which supply the flexors of the digits and fibres which supply the extensors, and yet when the whole of the fibres in the nerve root are simultaneously and equally excited flexion of the digits is brought about owing to the flexor muscles predominating over the extensors. This predominance of one group over another does not always obtain, however, as in the case of the ankle joint, where both the flexors and extensors are supplied by nerve fibres derived from the 6th lumbar root; simultaneous and equal excitation of all the fibres contained in this root causes the foot to be fixed at right angles at the ankle, neither the flexors nor the extensors predominating, but the one set of muscles equalising the action of the opposite set.

When a certain group of muscles is found to predominate in its action in one root it, as a rule, predominates in that root, *e.g.*, I have not met with an instance in which the flexors of the digits did not predominate over the extensors in their action when the 6th lumbar nerve root was stimulated.

If the muscles producing flexion of a certain joint predominate in their action in one root, those producing extension predominate in another. This does not, of course, apply only to when both the opposing groups of muscles are represented in two nerve roots, but also when they are represented in different nerve roots. We have seen, for instance, that in the case of the ankle joint the muscles producing dorsiflexion are represented in the 5th and 6th lumbar nerve roots, while those producing extension at the same joint are represented in the 6th and 7th lumbar roots. This being the case, dorsiflexion results on excitation of the 5th lumbar root, and extension results on excitation of the 7th.

When two opposed movements are represented in three consecutive nerve roots, the middle root of the series is that in which both movements are represented, while the root above contains the one movement and that below contains the other. Sometimes the two move-

* *Cf.* Patterson, Forgue, &c., *loc. cit.*

ments represented in the middle root of the series cancel each other, as it were, so that neither predominates, as in the case of flexion and extension at the ankle as represented in the 6th lumbar root. But when the muscles producing the one movement predominate over those producing the opposite one, in my experience those muscles always predominate in that root, *e.g.*, the flexors of the digits in the 6th lumbar root.

As regards the order in which flexion and extension at the various joints are represented in their relationship to the spinal level, we find the following to be the order in the fore limb of the dog.

Flexion at the shoulder.*
Flexion at the elbow.
Extension at the shoulder.
Extension at the wrist.
Flexion at the wrist.
Extension at the elbow.
Extension at the digital joints.
Flexion at the digital joints.

Thus, while flexion is represented at a higher level than extension for the upper segments of the limb, the reverse obtains for the lower segments of the limb.

The following is the order of representation of these movements as regards the spinal level in the posterior extremity of the dog and monkey:—

Flexion at the hip.
Extension at the knee.
Flexion at the ankle.
Extension at the digital joints.
Flexion at the knee.
Extension at the hip.
Extension at the ankle.
Flexion at the digital joints.

Here the arrangement as regards the segments of the limb is an alternate one, flexion of the highest segment coming first, then extension of the next segment; while for the lower segments flexion again comes first, and is followed by extension for the next or terminal segment of the limbs.

So that in comparing the order of representation of movements of the posterior with that of the anterior extremity it is found that the highest segments coincide by having flexion as the highest representation, but that none of the other segments thus coincide, until the

* For purposes of comparison the forward movement of the limb at the shoulder joint is called flexion, while the backward movement is called extension.

terminal segments are reached, when extension is represented at a higher level than flexion in both instances. This is, however, not strictly accurate, for dorsiflexion at the ankle is strictly analogous to extension at the wrist; which leaves two joints alone at which there is any discord, viz., the elbow and knee.

It is possible by stimulation of a single bundle of fibres in a nerve root to produce contraction of a single muscle and it alone; but this effect is easier to obtain in the case of the cervico-dorsal roots which enter into the formation of the brachial plexus than it is in the case of the roots which combine to form the lumbo-sacral plexus, owing to the difficulty of isolating the separate bundles of nerve fibres of which the roots are composed for a great enough distance of their course after their exit from the neural canal, and before they unite to form the plexus in the case of the lumbo-sacral roots. The same muscle is always represented in more than one nerve root, usually two, and to an unequal extent in these. The only muscle which I have met with which is not represented in more than one nerve root is the tensor fasciæ femoris; and this agrees with Sherrington's observations with regard to this muscle. In coming to the conclusion that the rule is that a single muscle is represented in neither more nor less than two nerve roots, I wish it to be clearly understood that this conclusion is based upon the results obtained in any single individual of a class under observation. That, owing to variations, the same muscle may be found represented in three or even four nerve roots, I do not pretend to deny; but what I contend is that in the majority of instances a single muscle is represented in two nerve roots, and that when a variation is met with with regard to this muscle, it is, as a rule, that one of the nerve roots in which it is represented is different, rather than that it is represented in more nerve roots.

When the same muscle is represented in two nerve roots the muscle fibres innervated by one root are not innervated by the other; so that only part of the muscle contracts when a single root is excited. This part of the muscle may be either one end of it, one lateral half of it, or a superficial or deep part of it, as the case may be.

Ablation Experiments.

Division of any given nerve root produces paresis of the group of muscles supplied by it, which paresis is temporary, nearly all of it being recovered from. The amount of paresis or paralysis produced is proportional to the number of nerve roots divided; and this again varies according to whether the roots divided are consecutive or alternate ones, the effect being much greater in the former than in the latter case. That such should be the case is only what was to be expected, for section of any two consecutive roots cannot fail to cause

paralysis of certain muscles, if my observations with regard to the representation of muscles in the nerve roots are correct; whereas section of alternate roots, while causing paresis of more muscles, cannot produce paralysis of any one, the tensor fasciæ femoris being excepted. Such division of one or more nerve roots does not result in incoordination of the remaining muscular combinations represented in other nerve roots; the remaining movements are merely more feeble.

Exclusion of a certain Root or Roots during an Epileptic Spasm in the Limb.

Division of one or more nerve roots produces alteration of the position of a limb during an epileptic spasm, which altered position depends on the muscular combinations that have been thus thrown out of action. And the effect is identical when the root or roots are divided at the time that the convulsions are evoked, and when they have been divided some weeks previously, *i.e.*, the position assumed by the limb on one side of the body in which the root or roots are divided previously is identical to that assumed by its fellow of the opposite side, the root or roots of which are divided at the time that the convulsions are induced. No incoordination is produced in the action of the remaining muscular combinations; and there is no evidence of overflow of the impulses which ought to travel down the divided root into other channels through the spinal centres so as to reach the muscles by new paths.

LIST OF PREVIOUS EXPERIMENTAL RESEARCHES ON THE LUMBO-SACRAL PLEXUS.

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DESCRIPTION OF FIGURES.

FIG. 1.—From a photograph of the most common type of lumbo-sacral plexus met with in *Macacus rhesus*. Shows the lumbo-sacral cord, the nerve roots which

spring from one side of it, and the nerve trunks derived from these nerve roots. The 5th lumbar root sends a branch to the sciatic nerve in this type of plexus, and both the obturator and anterior crural nerves are derived from the 4th and 5th lumbar roots. The branch which appears to spring from the 3rd lumbar root and to pass to the 4th lumbar root, in the figure, is in reality a branch which has its origin from the 4th lumbar root, and which, together with the 3rd lumbar root, forms the external cutaneous nerve.

Sp.C. = Spinal cord.
I.L. = 1st lumbar nerve root.
I.S. = 1st sacral nerve root.
E.C. = External cutaneous nerve.
A.C. = Anterior crural nerve.
Obt. = Obturator nerve.
Sc. = Sciatic nerve.
Sc.′ = Division of sciatic nerve which supplies the hamstring muscles.

FIG. 2.—From a photograph of the type of lumbo-sacral plexus which is the most common variation met with in *Macacus rhesus*. The lumbo-sacral cord is represented with the nerve roots which arise from one side of it and the nerve trunks which have their origin from these nerve roots. The 5th lumbar root does not send a branch to the sciatic nerve, nor does the 2nd sacral nerve root do so. The obturator nerve receives a slender branch from the 6th lumbar root in addition to those derived from the 4th and 5th lumbar roots. The anterior crural nerve is formed from the 4th and 5th lumbar roots, while the external cutaneous is formed from the 3rd and 4th lumbar roots; and the 4th lumbar root receives a branch from the 3rd lumbar root, before it gives off any of its own branches.

Sp.C. = Spinal cord.
I.L. = 1st lumbar nerve root.
I.S. = 1st sacral nerve root.
E.C. = External cutaneous nerve.
A.C. = Anterior crural nerve.
Obt. = Obturator nerve.
Sc. = Sciatic nerve.

FIG. 3.—From a photograph of a lumbo-sacral plexus of *Macacus rhesus* of the same type as the last, intended to show how in some instances the 2nd sacral nerve root might be erroneously supposed to send a branch to the sciatic nerve, a fallacy which can only be avoided by more minute dissection.

Sp.C. = Spinal cord.
II.L. = 2nd lumbar nerve root.
I.S. = 1st sacral nerve root.
E.C. = External cutaneous nerve.
A.C. = Anterior crural nerve.
Obt. = Obturator nerve.
Sc. = Sciatic nerve.
Sc.′ = Division of sciatic nerve which supplies the hamstring muscles.

FIG. 4.—From another photograph of the most common type of lumbo-sacral plexus met with in *Macacus rhesus*, chiefly meant to show how slender the branch from the 5th to the 6th lumbar nerve root is in some cases.

Sp.C. = Spinal cord.

III.L., IV.L., V.L., VI.L., VII.L. = 3rd to 7th lumbar nerve roots.

I.S., II.S. = 1st and 2nd sacral nerve roots.

E.C. = External cutaneous nerve.

A.C. = Anterior crural nerve.

Obt. = Obturator nerve.

Sc. = Sciatic nerve.

× = Branch from 5th to 6th lumbar nerve root.

"A New Hypothesis concerning Vision." By JOHN BERRY HAYCRAFT, M.D., D.Sc. Communicated by E. A. SCHÄFER, F.R.S. Received February 16,—Read March 2, 1893.

(Abstract.)

It is suggested that many of the well-known facts of vision can be more easily understood when studied from the evolutionary standpoint. The eye is no exception to the general rule, accepted by evolutionists, that all parts of the body are gradually evolved under the environmental conditions of the species. Many species are devoid of a colour sense, but are able, nevertheless, to distinguish light from darkness, and where a colour sense is present it has been developed in relationship with environmental pigments : these points have been brought out with especial clearness by Darwin and Lubbock. We may infer, therefore, that the visual apparatus of a colour-seeing species—man, for instance—was at one time only able to distinguish light from darkness, and that the colours red, yellow, green, &c., were once seen as grey. This enables us to understand why it is that the outer, less used, parts of the retina are at the present day colour blind ; this fact fits in at once with our evolutionary hypothesis. From the same point of view we may explain why a minimal stimulus from a red, green, or other coloured object gives rise merely to the sensation grey—"bei Nacht sind alle Kätzen grau"—even when it falls upon the centre of the retina. In this case the minimal stimulus is unable to excite more than the simple sensation of light, and the quality of this light is not seen. A parallel may in fact be drawn between sight and hearing and smell, for we may hear a sound too feebly to assign to it its pitch, and we may have to sniff a faint odour in order to make out exactly what it is. But a red, yellow, or green object, very brightly illuminated, also appears white, and this has been explained in various ingenious ways. It is suggested, however, that this is merely a special case of

Fig. 1.

FIG 2.

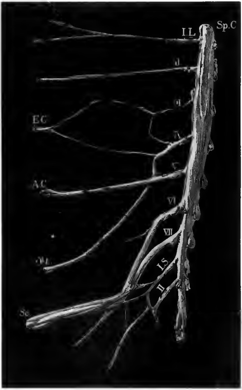

Fig. 3.

FIG. 4.